Visual processing of social information during interocular suppression

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Abstract
We studied the processing of socially relevant visual stimuli during continuous flash suppression (CFS), a potent interocular suppression technique that we used to render stimuli invisible. In Studies 1–6, we measured the duration of perceptual suppression during CFS to test whether socially relevant stimuli have privileged access to visual awareness. Study 1 demonstrated that face detection in adult observers is modulated by facial properties previously shown to modulate looking preferences in newborns. Study 2 revealed own-race and own-age biases in face detection, indicating that visual awareness of faces is shaped by visual experience with one's own social group. In Study 3, we found larger effects of stimulus inversion on the detection of human faces and bodies than for other familiar objects, suggesting that detection mechanisms are preferentially tuned to conspecifics. Study 4 showed that faces with direct gaze are detected more quickly than faces with averted gaze. Study 5 revealed a confounding factor in schematic emotional faces that are considered to be well-controlled visual stimuli. In Study 6, we found that faster detection of fearful compared to neutral faces relies on high spatial frequencies, arguing against a functional role of a subcortical pathway to the amygdala. Study 7 showed that measures of visual detection during CFS cannot provide unequivocal evidence for unconscious processing under CFS. In Studies 8 and 9 we therefore measured adaptation aftereffects from stimuli rendered permanently invisible by CFS. In Study 8, we measured face shape aftereffects and found that only low-level monocular components of face shape adaptation can proceed unconsciously, whereas higher-level components depend on visual awareness. Study 9 revealed that only size-dependent low-level components of eye gaze can be represented unconsciously, while object-centered higher-level representations of eye gaze directions require visual awareness.

Keywords: Visual awareness, interocular suppression, faces, bodies, eye gaze, facial expressions

Zusammenfassung
Wir untersuchten die Verarbeitung sozial relevanter visueller Reize während “continuous flash suppression” (CFS), einer besonders wirkungsvollen Technik der interokularen Unterdrückung, die benutzt wird um Reize unsichtbar zu machen. In den Studien 1–6 maßen wir die Dauer der perzeptuellen Unterdrückung während CFS um zu testen, ob sozial relevante Reize bevorzugten Zugang zum visuellen Bewusstsein haben. Studie 1 zeigte, dass die Detektion von Gesichtern bei Erwachsenen durch Gesichtsmerkmale beeinflusst wird, welche auch Blickpräferenzen von Neugeborenen beeinflussen. Studie 2 zeigte, dass Gesichtsdetektion durch die Ethnie und Altersgruppe des zu detektierenden Gesichtes beeinflusst wird. In Studie 3 fanden wir größere Effekte der Inversion auf die Detektion von menschlichen Gesichtern und Körpern als auf andere vertraute Objekte. In Studie 4 fanden wir, dass Gesichter mit direktem Blick schneller detektiert werden als Gesichter mit abgewandtem Blick. Studie 5 deckte einen konfundieren Faktor in schematischen emotionalen Gesichtern auf. In Studie 6 fanden wir, dass die schnellere Detektion von furchtsamen im Vergleich zu neutralen Gesichtern auf hohen Raumfrequenzen beruht. Studie 7 zeigte, dass die Messung der visuellen Detektion während CFS keinen eindeutigen Nachweis für unbewusste Verarbeitung unter CFS erbringen kann. In den Studien 8 und 9 maßen wir deshalb Adaptations-Nacheffekte von Reizen, die durch CFS dauerhaft unsichtbar gemacht wurden. Studie 8 zeigte, dass lediglich monokulare Komponenten der Gesichtsform-Adaptation unbewusst ablaufen können, während komplexere Komponenten auf visuelles Bewusstsein angewiesen sind. Studie 9 zeigte, dass nur größenabhängige Komponenten von Blickrichtungen unbewusst repräsentiert werden können, während objektzentrierte Repräsentationen von Blickrichtungen visuelles Bewusstsein benötigen.

Schlagwörter: Visuelles Bewusstsein, interokulare Suppression, Gesichter, Körper, Blickrichtungen, emotionale Gesichtsausdrücke

1 General introduction

"What consciousness does is to provide human beings with an extraordinarily effective tool for doing natural psychology" (Humphrey, 1987, p. 10).

Humans are extraordinarily social animals. Living in groups is central to human existence. Groups provide resources that are vital to reproduction and survival, such as protection against predators, childrearing, mutually beneficial social exchange, and a pool of potential partners for mating. However, an environment populated by other agents also presents challenges to the social animal. Because all agents follow their own goals, their behavior is often hard to predict. To successfully navigate our social world, it is therefore necessary to read others' mental and emotional states and to infer their intentions, that is, we need to do "natural psychology" (Humphrey, 1987). Nicholas Humphrey's provocative proposal is that the need for social intelligence in a complex social world has exerted selection pressure, resulting in increased brain size (Dunbar, 1998) and culminating in the emergence of consciousness (Humphrey, 1987).

Although highly speculative, the idea that consciousness reflects neural mechanisms that evolved to deal with the unpredictability of social environments and the complexities of social interactions is not inconsistent with current accounts of the functions of consciousness. Most views converge on the notion that consciousness is central to flexibly adjust behavior to novel situations and complex environmental demands, to monitor and communicate one's own internal state and to infer the mental state of other individuals (Baars & McGovern, 1996; Cleeremans, 2005; Crick & Koch, 2003; Koch & Tsuchiya, 2007). For example, in Baars' global workspace theory only conscious content is distributed to unconscious specialized expert systems which can then be combined to recruit all available cognitive resources in novel or unpredictable situations (Baars, 1988, 1997). Because at any given moment only one condensed set of events can have this privileged status of "fame in the brain" (Dennett, 2001) and be conscious, representations of external and internal stimuli and events compete for access to consciousness (Baars, 1997; James, 1890). To enable adaptive behavior, those representations that are particularly relevant to the organism's goals and to interactions with the environment should have privileged access to consciousness (James, 1890).

Here we asked whether the unique biological and social significance of other individuals is reflected in privileged access to consciousness for those visual stimuli that are diagnostic for the presence of other persons, such as human faces and human bodies, and for facial features that are central to social interaction and communication, such as eye gaze and facial expressions. Conversely, we hypothesized that some elaborate processing of complex features of socially relevant visual stimuli might be possible without accessing the capacity-limited stage of conscious awareness. We therefore tested whether specific facial features would be processed unconsciously.

While vision scientists had long focused almost exclusively on the coding of simple visual stimuli such as bars, gratings, moving dots or color patches, the discovery of face-selective cells in macaque inferotemporal cortex (Gross, Rocha-Miranda, & Bender, 1972) has stimulated tremendous interest in the visual processing of complex social stimuli, with faces now being the most frequently used visual stimuli in experimental psychology (Nakayama, 2011). This research has demonstrated that the relevance of other persons is reflected at multiple levels in the human visual system, and can already be observed in neonates who show a preference for cues that are diagnostic for the presence of other

individuals, such as faces and face-like patterns (Farroni et al., 2005; Goren, Sarty, & Wu, 1975; Johnson, Dziurawiec, Ellis, & Morton, 1991; Valenza, Simion, Macchi Cassia, & Umità, 1996), eye contact (Farroni, Csibra, Simion, & Johnson, 2002), biological motion (Simion, Regolin, & Bulf, 2008), and goal-directed actions (Craighero, Leo, Umiltà, & Simion, 2011). Together with innate neural connectivity patterns, such inborn preferences may subsequently lead to specialization at higher levels of processing (Johnson, Grossmann, & Cohen Kadosh, 2009; McKone, Kanwisher, & Duchaine, 2007), finally resulting in expert recognition of face identity, body postures, and mental states. Indeed, neuroimaging studies have described distinct cortical areas in the ventral visual pathway specialized for processing faces (Kanwisher & Yovel, 2006) and human bodies (Peelen & Downing, 2007).

It is clear from both everyday knowledge and a large body of literature that faces and bodies provide a wealth of information about another person's identity, age, gender, actions, attractiveness, direction of attention, intentions, and emotional state (Slaughter, Stone, & Reed, 2004). Whether the social relevance of other persons is reflected in social visual information having privileged access to visual awareness, however, has rarely been examined. This may be due to the fact that visual processing that precedes and leads to visual awareness is, by definition, inaccessible to introspection. Nevertheless, the rapid and accurate detection[1] of other persons has presumably been highly beneficial for adaptive behavior in human evolution and is an essential first step in social cognition and interaction.

1.1 Structure of the thesis

The next part of this Introduction will briefly introduce the experimental technique we used to study access to awareness and unconscious processing. Section 2 contains a summary and discussion of our empirical studies. Due to the wide range of topics, the presentation of the results from the different studies in Section 2 is preceded by a short introduction into the respective topic and the relevant literature to clarify the motivation of our specific research question. Section 2 also highlights the links between our studies and discusses apparently inconsistent findings. Finally, Section 3 provides some general conclusions and suggests directions for future research.

1.2 Interocular suppression

Vision scientists have developed psychophysical techniques that open a window into the competitive dynamics of neural assemblies (Koch, 2004) underlying conscious perception (Kim & Blake, 2005). For example, when dissimilar images are presented to the two eyes at corresponding visual field locations, observers typically experience perceptual alternations between the two images rather than perceiving one composite percept. This phenomenon of binocular rivalry is believed to result from reciprocal inhibition between neural representations of the two stimuli at multiple levels of the visual system (Sterzer, Kleinschmidt, & Rees, 2009; Tong, Meng, & Blake, 2006). The neural population representing the perceptually dominant stimulus exerts stronger inhibition, thereby suppressing the other stimulus from awareness. As the dominant neural population adapts

[1] Please note that the terms "access to awareness" and "detection" are used interchangeably throughout this thesis (Rafal, Danziger, Grossi, Machado, & Ward, 2002), both referring to measures of localization performance. Likewise, the expression "awareness of" a stimulus, e.g. faces, here is meant to be a shortened form of "access to awareness for" and does not mean that participants discriminated or identified the stimulus or the stimulus category.

over time, inhibition weakens until a perceptual switch occurs and the other stimulus achieves dominance (Alais, 2012; Alais, Cass, O'Shea, & Blake, 2010; Levelt, 1965). Since Crick and Koch (1998) proposed rivalry as a powerful tool for tracing the neural concomitants of visual awareness, many human neuroimaging and monkey neurophysiology studies have characterized the neural correlates of perceptual dominance and suppression (Baker, 2010; Lin & He, 2009; Sterzer et al., 2009; Tong et al., 2006). For our present purpose of measuring access to awareness and unconscious processing, however, conventional binocular rivalry was not optimally suited, because perceptual switches occur unpredictably, possibly due to neural noise (Wilson, 2003).

We therefore used continuous flash suppression (CFS, Tsuchiya & Koch, 2005), a potent interocular suppression technique that allows for long and reliable periods of suppression. In CFS, the perception of a foveally presented stimulus such as a face photograph can be completely suppressed by a train of colorful, high-contrast patterns flashed at about 10 Hz to the other eye (see Figure 1A). This period of invisibility can last for a couple of seconds – or even minutes (Tsuchiya & Koch, 2005) – until the stimulus finally overcomes suppression and gains access to awareness. Suppression during CFS is much deeper than during binocular rivalry (Tsuchiya, Koch, Gilroy, & Blake, 2006). Although it seems straightforward to attribute the effectiveness and depth of CFS to the fact that the continuously flashing masks prevent the corresponding neural representations from being adapted, it is not yet clear whether CFS should be regarded as a particularly effective variant of binocular rivalry (Shimaoka & Kaneko, 2011) or whether CFS involves distinct mechanisms (Tsuchiya et al., 2006).

In the present studies we employed CFS in two ways. In Studies 1–7 we recorded the duration of perceptual suppression during CFS as a measure of detection performance for different stimuli (see Figure 1A). In these studies, participants were asked to localize an initially invisible stimulus as quickly and accurately as possible (Jiang, Costello, & He, 2007). Recent studies have demonstrated that this detection paradigm is a powerful and sensitive device to probe potency of stimuli to gain access to visual awareness. For example, upright faces and words are suppressed for shorter durations than inverted (i.e., rotated by 180°) faces and words (Jiang et al., 2007; Yang & Yeh, 2011). Suppression durations have also been found to be modulated by emotional facial expressions (Sterzer, Hilgenfeldt, Freudenberg, Bermpohl, & Adli, 2011; Tsuchiya, Moradi, Felsen, Yamazaki, & Adolphs, 2009; Yang, Zald, & Blake, 2007), emotional words (Yang & Yeh, 2011), semantic priming (Costello, Jiang, Baartman, McGlennen, & He, 2009), natural scene content (Mudrik, Breska, Lamy, & Deouell, 2011), and by congruency with concurrently presented odors (Zhou, Jiang, He, & Chen, 2010b). One challenge to comparing detection performance among different stimulus conditions is that suppression durations are strongly influenced by physical stimulus "strength" (e.g., contrast, luminance, spatial frequency). Even when mean luminance, global contrast and spatial frequency content are equated across conditions, local physical stimulus differences can still affect suppression durations (Yang et al., 2007). The influence of such factors and how to control for them is therefore repeatedly addressed in Section 2.

In Studies 8 and 9 we took a different approach and tested whether facial features continue to be processed when rendered permanently invisible by CFS. Whereas many recent studies found that basic stimulus features such as orientation, spatial frequency, color or translational motion can be processed despite suppression (Lin & He, 2009), it remains unclear to what extent more complex visual information such as faces or facial features can be represented without awareness under interocular suppression. There is only some limited evidence that specific stimulus attributes related to emotional or highly arousing stimuli

(Adams, Gray, Garner, & Graf, 2010; Jiang, Costello, Fang, Huang, & He, 2006; Yang et al., 2011), manipulable objects (Almeida, Mahon, & Caramazza, 2010; Almeida, Mahon, Nakayama, & Caramazza, 2011), and numerical information (Bahrami et al., 2010) can escape suppression and remain behaviorally effective.

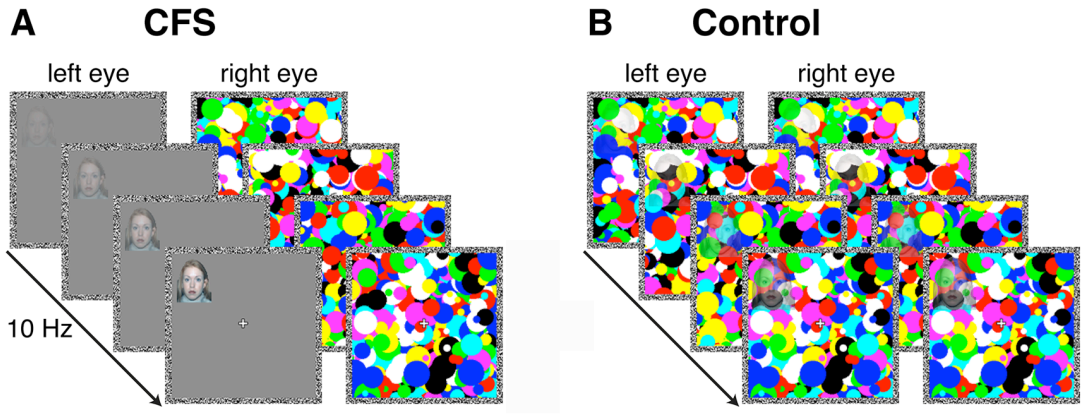

Figure 1. (A) Schematic of the experimental protocol to measure suppression durations during CFS. To induce interocular suppression, high contrast CFS masks flashing at 10 Hz are presented to one eye, while a test stimulus, for example a face, is gradually introduced to the other eye. At the beginning of a trial, the test stimulus is invisible. Observers are asked to indicate as quickly and accurately as possible the location in which the test stimulus or any part of it becomes visible. (B) Schematic of the binocular control condition (see Section 2.4) in which the same stimuli as during CFS are presented binocularly and the test stimulus is presented transparently on top of the masks. Transparency is gradually reduced over the course of a trial.

2 Summary and discussion of empirical studies

In Studies 1–3 we measured the detection of visual information that is diagnostic for the presence of conspecifics – human faces and human bodies. In Studies 4–6 we investigated the influence of eye contact and emotion on visual awareness of faces. Study 7 represents a methodological excursion to critically evaluate whether perceptual suppression during CFS can be taken as a marker of unconscious processing during interocular suppression. Finally, in Studies 8 and 9 we probed adaptation aftereffects from face shape and eye gaze rendered permanently invisible by CFS.

2.1 Visual awareness of faces: Functional mechanisms (Studies 1 and 2)

Faces provide a rich source of social information. Before we can make full use of this information, however, we need to localize a face in the visual field. In the first two studies we investigated which facial properties determine whether we detect and thus consciously perceive another person's face. Whereas countless studies have examined how we identify and remember individual faces, surprisingly little is known about the perceptual mechanisms that govern the simple detection of a face. The most influential models of face perception have focused exclusively on the cognitive and neural mechanisms that process faces only after they have been detected and categorized as faces (Bruce & Young, 1986; Burton, Bruce, & Hancock, 1999; Haxby, Hoffman, & Gobbini, 2000; Valentine & Endo, 1992). By contrast, in machine vision it is natural to draw a distinction between an initial stage of face detection and a subsequent process of face recognition (Hjelmås & Low, 2001; Viola & Jones, 2004),

as detection and recognition have fundamentally different computational goals. Whereas face recognition depends on fine-grained facial information that distinguishes individual faces, detection mechanisms need to be sensitive to visual information that is common to all faces. Only recently, neuropsychological studies on individuals with acquired and developmental prosopagnosia have revealed a dissociation between face detection and face recognition abilities in the human visual system (Duchaine & Nakayama, 2006). Prosopagnosic individuals show severe deficits in face recognition, but perform well in face detection tasks (de Gelder & Rouw, 2000; Garrido, Duchaine, & Nakayama, 2008; Le Grand et al., 2006).

As a consequence, some more recent account of face perception now incorporate a distinct initial stage of face detection in a hierarchy of face processing stages (de Gelder, Frissen, Barton, & Hadjikhani, 2003; Grill-Spector & Kanwisher, 2005; Johnson, 2005; Tsao & Livingstone, 2008). For example, the model by Tsao and Livingstone (2008) holds that certain visually responsive neurons early in the face processing hierarchy are specifically tuned to detect face-related information in the visual input and to segment faces from the background. These face detection mechanisms are assumed to act as domain-specific filters, passing visual information to downstream face-specific recognition mechanisms only when the input contains features indicative of a face. Accordingly, face detection is fundamental to all subsequent, more elaborate processing steps such as identification, social categorization or long-term memory encoding.

How can such face detection mechanisms localize regions in the visual field that contain a face? Because all faces share the same global structure, face detection can efficiently be achieved by matching the visual input to an internal representation corresponding to the structure of a prototypical upright face (Lewis & Ellis, 2003; Tsao & Livingstone, 2008). This internal "face template" is assumed to represent the "first-order relations" between facial features that are invariant across different face exemplars (e.g., two eyes above nose above mouth; Maurer, Le Grand, & Mondloch, 2002; McKone et al., 2007; Tsao & Livingstone, 2008). Indeed, when these spatial relations among facial parts are distorted by turning faces upside down, face detection performance declines (Garrido et al., 2008; Lewis & Edmonds, 2003; Purcell & Stewart, 1988; Tyler & Chen, 2006). As upright and inverted faces consist of physically identical features, this face inversion effect (FIE) supports the notion that face detection critically depends on information about the relative spatial arrangement of facial features. In other words, the goodness of fit between the visual input and the internal face template is supposed to determine access to conscious awareness. A poor fit could account for the decline in detection performance for inverted faces (Lewis & Ellis, 2003; Purcell & Stewart, 1988).

The comparison of physically identical upright and inverted stimuli is an elegant way to examine the mechanisms that govern access to visual awareness, because the confounding influence of potential differences in low-level physical stimulus properties is ruled out. Moreover, following the idea that face detection involves matching the visual input to an upright (deformable) face template (Lewis & Edmonds, 2003; McKone et al., 2007; Tsao & Livingstone, 2008), the difference in detection performance for upright and inverted faces, i.e. the FIE, can be regarded as reflecting the goodness of fit of a given face stimulus to the internal template. Thus, we used the size of the FIE as a quantification of how well early perceptual mechanisms supporting visual awareness of faces are tuned to different face-related visual input.

To measure the effect of face inversion on simple detection, we used CFS to render upright or inverted faces invisible at the beginning of each trial and recorded the time participants needed to localize the initially invisible stimulus. Previous studies found that

upright faces overcome CFS and break into awareness considerably more quickly than inverted faces (Jiang et al., 2007; Zhou et al., 2010a). This CFS technique may therefore be particularly well suited to reveal visual information used to detect a face. We approached this question from two different angles. In the first study, we asked whether face detection mechanisms in adults share similarities with innate face preferences. In the second study, we took an opposite approach and tested whether visual experience with faces from one's own social groups facilitates access to visual awareness.

2.1.1 Similarities between face detection in adults and newborns' looking preferences (Study 1)

We examined whether face detection in adults relies on facial properties similar to those underlying newborns' looking preference for faces and face-like stimuli (Goren et al., 1975; Johnson et al., 1991; Valenza et al., 1996). Importantly, neonates preferentially look at upright compared to inverted faces (Farroni et al., 2005). This has led to notion of an inborn face template representing the facial structure that drives the early development of face-specific neural structures and might serve to detect faces throughout life (McKone et al., 2007; Tomalski, Csibra, & Johnson, 2009a; Tomalski, Johnson, & Csibra, 2009b). We tested two central predictions from the hypothesis that the advantage of upright faces in gaining access to awareness during CFS reflects perceptual mechanisms similar to those critical to elicit newborns' orienting biases towards upright faces (Stein, Peelen, & Sterzer, 2011b).

First, newborns' preference for upright over inverted faces is abolished when faces are contrast-reversed or lit from below (Farroni et al., 2005), indicating that the putative innate face template does not only represent first-order relations between facial features, but also ordinal contrast relationships characteristic for faces under natural viewing conditions. Similarly, our findings suggest that face detection in adults does not only rely on the extraction of first-order relations between facial features, but is also highly sensitive to contrast relations within the face. In three experiments, we found the size of the FIE to be reduced when these ordinal contrast relationships were distorted by contrast reversal or bottom-up lighting.

Second, looking biases in newborns can be elicited even by simple head-shaped patterns containing only three dark blobs representing the upright configuration of the eyes and the mouth (Johnson et al., 1991; Morton & Johnson, 1991), and this effect is not seen for contrast-reversed patterns (Farroni et al., 2005). This suggests that coarse face-like visual information, possibly conveyed by a subcortical face detection pathway (Johnson, 2005), is sufficient to trigger newborns' looking biases. In an additional experiment, we found that such simple head-shaped patterns were perceptually suppressed for longer periods when the arrangement of the blobs representing the eyes and the mouth was inverted, and this inversion effect was reduced for contrast-reversed face-like patterns.

Interestingly, there was no difference in detection times for upright and inverted face-like patterns in a binocular control experiment not involving interocular suppression (for an example, see Figure 1A). The increased sensitivity of the CFS technique to inversion may reflect CFS-specific unconscious processing differences between upright and inverted stimuli (Jiang et al., 2007; Zhou et al., 2010a; but see Section 2.4). Faces rendered invisible by interocular suppression have been found to activate subcortical structures such as the amygdala in the absence of corresponding ventral visual cortex activity (Jiang & He, 2006; Pasley, Mayes, & Schultz, 2004; Williams, Morris, McGlone, Abbott, & Mattingley, 2004). Thus, it could be speculated that the advantage of upright face-like patterns in gaining access to awareness involves a subcortical face detection pathway that is supposed to trigger

newborns' orienting biases towards faces and that remains functional in the adult brain (Johnson, 2005).

In summary, our results indicate a close similarity between the facial attributes that are central to visual awareness of faces in adults and the facial properties that attract newborns' gaze.

2.1.2 Own-race and own-age biases in face detection (Study 2)

These findings suggest that the perceptual mechanisms underlying face detection are broadly tuned to register all visual information that could be indicative of an upright face under natural lighting conditions. Thus, it is possible that relatively hard-wired face detection mechanisms respond to all visual patterns that contain the first-order relations and the normal contrast relations of upright faces (Johnson, 2005; McKone et al., 2007; Tomalski et al., 2009a). An alternative possibility is that the perceptual mechanisms mediating simple detection at the initial stage of face processing are modified by visual experience and more narrowly tuned to those faces that have been encountered most frequently. Indeed, the inversion effects obtained in the previous experiments were not of equal size across all conditions, but were larger for naturalistic face stimuli than for simple face-like patterns.

Studies on face recognition have demonstrated that – despite the remarkable ability of human observers to discriminate and remember a myriad of individual faces – such face expertise does not equally encompass all kinds of faces. Perhaps most famously, people have difficulty recognizing faces of a race group other than their own (Meissner & Brigham, 2001). Similarly, observers are worse at recognizing faces of other ages compared to their own age group (Rhodes & Anastasi, 2011). These in-group advantages are assumed to reflect extensive visual experience with faces from one's own social group that tunes face recognition mechanisms to the more familiar morphology of in-group faces (Rossion & Michel, 2011). As a consequence, in-group faces are processed in a less holistic, more piecemeal and hence less efficient way (de Heering & Rossion, 2008; Michel, Rossion, Han, Chung, & Caldara, 2006; Tanaka, Kiefer, & Bukach, 2004). We tested whether such processing advantages for in-group faces would manifest at the initial stage of face detection.

In two experiments, we had young Caucasian adults detect same-race and other-race faces as well as same-age and other-age faces under CFS (Stein, End, & Sterzer, submitted). Suppression durations revealed large differences in the size of the FIE depending on social category. For faces from the participants' own race and age group the FIE was about twice as large as the FIE for faces from other race and age groups. Although we tested young Caucasian adults only, the comparison of identical upright and inverted faces within each face category rules out the possibility that this early perceptual bias for upright in-group faces was driven by low-level physical stimulus differences between face categories. Thus, these findings suggest that social categories modulate the initial stage of face processing, and thereby influence whether we see another person's face in the first place.

The impact of social categories on face detection demonstrates that the human visual system does not work like many machine vision algorithms that detect faces by matching the input to a coarse face template. Rather, these own-race and own-age biases are consistent with the "experienced-based holistic account" by Rossion and Michel (2011) which holds that both memory as well as perceptual deficits for other-race (and potentially other-age) faces result from a poor match between the faces' unfamiliar morphology and an experience-derived template representing the global structure of an average of all faces known to the observer. Nevertheless, this account is compatible with the idea that an innate face template may serve as the basis for the subsequent fine-tuning of face detection mechanisms according to the

specific social environment, and leaves open the possibility that traces of inborn face detection mechanisms may be preserved in the adult visual system.

2.2 Visual awareness of conspecifics: Inversion effects for bodies (Study 3)

Besides from these specific functional considerations, the strong effect of face inversion on the duration of perceptual suppression in itself demonstrates that the visual system is extremely sensitive to face-related visual information. In fact, it has been argued that inversion effects in simple detection are restricted to faces (Zhou et al., 2010a) and rely on the unconscious extraction of structural facial information in cortical areas that are specialized for face processing (Jiang et al., 2007; Zhou et al., 2010a), such as the fusiform face area (Kanwisher, McDermott, & Chun, 1997). It is possible that such-face specific detection mechanisms operating outside of conscious awareness have evolved to rapidly detect the presence of other individuals in the visual field. In addition to another person's face, however, another important stimulus that signals the presence of conspecifics is the human body.

Indeed, there are a number of similarities between the visual processing of faces and bodies. First, both faces and bodies capture attention and are processed with higher priority than other objects (Downing, Bray, Rogers, & Childs, 2004; Langton, Law, Burton, & Schweinberger, 2008; Lavie, Ro, & Russell, 2003; Ro, Friggel, & Lavie, 2007). Second, human neuroimaging studies have not only identified face-selective cortical areas such as the FFA, but also distinct body-selective cortical regions, namely the adjacent and spatially overlapping fusiform body area (Peelen & Downing, 2005; Schwarzlose, Baker, & Kanwisher, 2005) and the extrastriate body area (Downing, Jiang, Shuman, & Kanwisher, 2001). Finally, the recognition of faces and bodies, more strongly than the perception of other objects, relies on the extraction of configurations of features rather than individual features in isolation (Minnebusch & Daum, 2009). In recognition tasks, inversion does not only interfere with face discrimination (Yin, 1969; Robbins & McKone, 2007), but also with the discrimination of individual bodies (Reed, Stone, Bozova, & Tanaka, 2003; Reed, Stone, Grubb, McGoldrick, 2006), albeit to a lesser degree (Minnebusch & Daum, 2009). It is has been unknown, however, whether inversion of bodies, like faces, influences perception at the initial detection stage. We hypothesized that if perceptual mechanisms specialized for the detection of persons in their normal upright orientation exist, inversion may affect the earliest levels of visual body processing in a similar way as it affects face detection.

In a series of seven experiments we measured the effect of inversion on the duration of perceptual suppression during CFS for bodies, faces, and other familiar animate and inanimate object categories (Stein, Sterzer, & Peelen, 2012b). Upright bodies were detected considerably more quickly then inverted bodies, independent of whether they were presented as headless photographs or as silhouettes without facial information. This body inversion effect (BIE) persisted at full strength for silhouettes depicting highly variable and asymmetrical postures seen from various viewpoints. By contrast, no BIE was found when we randomly reattached body parts in their upright position to the trunk, indicating that the spatial relations of the body parts relative to the trunk are necessary to activate body detection mechanisms. Importantly, the BIE was larger than the effect of inversion on the detection of other familiar object categories (chairs, table lamps, home plants, trees). Furthermore, a general detection advantage for animate objects (New, Cosmides, & Tooby, 2007; Tipples, Young, Quinlan, Broks, & Ellis, 2002) is unlikely to account for this effect, as the BIE was also larger than inversion effects for chimpanzee faces, dogs and birds. Finally, in three experiments we directly compared the size of the BIE to the FIE for human faces and found no significant differences.

This pattern of results – similar BIE and FIE without comparable effects for other familiar objects – indicates that early stages of visual perception that mediate access to awareness are preferentially tuned to both upright human faces and human bodies, i.e. to cues that signal the presence of conspecifics (see Figure 2).

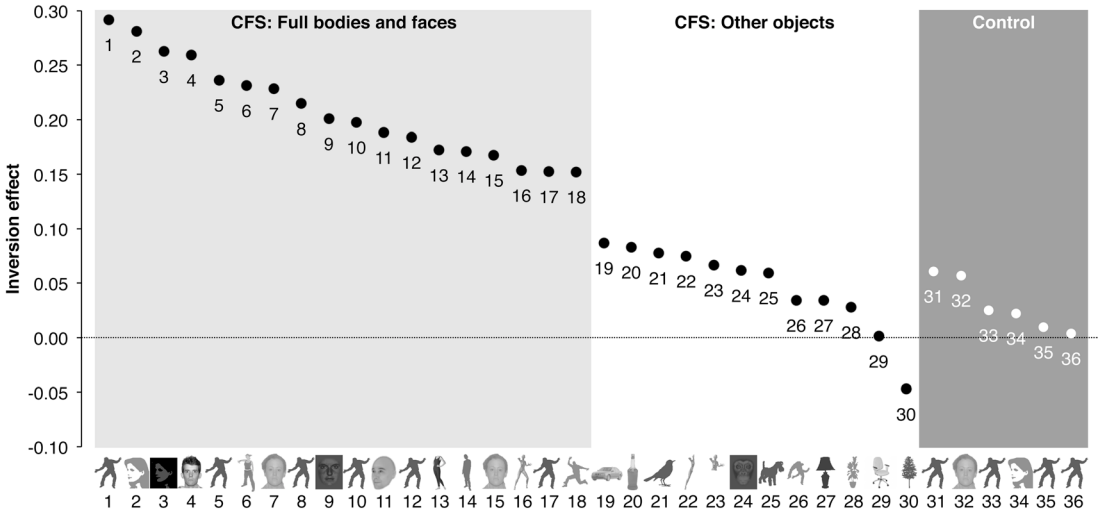

Figure 2. Inversion effects for human bodies and faces, other objects (animate and inanimate) obtained under CFS and during a binocular control condition not involving interocular suppression. For each subject and each stimulus condition, normalized effects were obtained by dividing the difference between mean response times for upright and inverted test stimuli by the mean response time for inverted stimuli (Tsuchiya et al., 2009). Points denote the respective inversion effect averaged across subjects. Thumbnails depict an example stimulus from each category. Numbers below the points refer to the numbers below the associated thumbnails. Please note that this overview includes data from a number of additional experiments that are not reported in the manuscript (Stein et al., 2012b), for example vertically and horizontally cut bodies, Mooney-like faces, cars, or bottles.

2.3 Facial features modulate visual awareness of faces: Eye contact and emotion (Studies 4–6)

There are, however, some more specific visual cues displayed by conspecifics that can dynamically change according to the social context and may therefore be particularly important for social communication and adaptive behavior. Two such cues are facial expressions and eye gaze directions.

2.3.1 Eye contact facilitates awareness of faces (Study 4)

Eye gaze is central to social interactions, in that is provides information about another person's emotional and cognitive state, goals, intentions and direction of attention (Allison, Puce, & McCarthy, 2000; Baron-Cohen, 1997; Itier & Batty, 2009; Nummenmaa & Calder, 2008). The perception of direct and averted gaze is associated with partially distinct cognitive processes. While the perception of averted gaze is primarily associated with attentional shifts that can occur in a relatively reflexive manner (Frischen, Bayliss, & Tipper, 2007), direct gaze signals that the observer is the current center of attention and interest (George & Conty, 2008). In many non-human animals, direct gaze indicates threat and triggers defensive

responses (Emery, 2000). By contrast, in humans eye contact serves to initiate social communication and to establish joint attention.

Converging lines of evidence suggest that this evolutionary and social relevance of direct gaze is reflected in the human visual system. Already in the first few days of life, infants prefer faces making eye contact over faces with averted gaze (Farroni et al., 2002). In adults, faces with direct gaze attract and hold spatial attention (von Grünau & Anston, 1995; Senju & Hasegawa, 2005; Senju, Hasegawa, & Tojo, 2005). This processing advantage for faces with direct gaze, referred to as the "eye contact effect" has been proposed to be mediated by a fast subcortical pathway involving the amygdala which then modulates cortical gaze-processing areas such as superior temporal sulcus (STS; Senju & Johnson, 2009). Because neuroimaging studies on face processing under interocular suppression revealed residual activity in both the amygdala (Jiang & He, 2006; Pasley et al., 2004; Williams et al., 2004) and the STS (Jiang & He, 2006), we hypothesized that eye contact may be extracted under interocular suppression and modulate access to visual awareness for faces rendered initially invisible through CFS (Stein, Senju, Peelen, & Sterzer, 2011c).

We used a set of face stimuli that controlled for the influence of eye symmetry in faces with direct gaze and straight head orientation. Face stimuli with averted and direct gaze were constructed from the same models with laterally averted heads. Eye regions containing eyes that were directed either maximally to the left or to the right were derived from other photographs of the same persons and then superimposed on the base images. This yielded the impression of direct gaze when eye gaze and head were oriented in opposite directions and the impression of averted gaze when eye gaze and head were pointing in the same direction. In a series of experiments, we measured the time participants needed to localize these face stimuli under CFS. Suppression durations were consistently shorter for faces making eye contact with the observer than for faces with averted gaze.

Thus, faces with direct gaze have an advantage in gaining access to awareness, enabling the rapid detection of other individuals making eye contact with the observer. These findings are consistent with shorter suppression durations for other ecologically relevant facial information, such as fearful expressions (Tsuchiya et al., 2009; Yang et al., 2007). What is more, the effect of eye contact on access to visual awareness suggests that early visual processing occurring before conscious detection does not only prepare the organism for fight-or-flight responses to threat signals, but also for social contact and communication.

2.3.2 A confound in schematic emotional faces (Study 5)

Whereas the comparison of faces with direct and averted gaze allowed us to control for the potential influence of low-level physical stimulus properties, this is more difficult or even virtually impossible to achieve for naturalistic face stimuli with different facial expressions that necessarily differ along physical dimensions. For example, even when fearful and neutral face photographs are matched on global contrast and mean luminance, larger eye whites in fearful faces can cause better detection (Yang et al., 2007). Since Purcell, Stewart, and Skov (1996) showed that similar low-level differences between face photographs could account for the "anger superiority" effect, i.e. efficient visual search for an angry face in an array of happy faces (Hansen & Hansen, 1988), researchers studying the visual processing of emotional faces have been very cautious about such confounding physical stimulus differences. As a consequence, numerous studies have used schematic line-drawings of faces instead of face photographs (Frischen, Eastwood, & Smilek, 2008; Horstmann, 2007). Because schematic faces representing facial expressions differ only in the orientation of the

line-drawn "facial features" such as the mouth curve, they are believed to convey different emotional meanings in the absence of low-level physical stimulus differences.

Motivated by the overarching view that threatening or negatively charged facial expressions capture attention and receive prioritized processing (Öhman & Mineka, 2001; Tamietto & de Gelder, 2010; Vuilleumier & Driver, 2007), many studies compared visual search for negative ("smileys" with an inverted mouth curve) and positive ("smileys") schematic faces. However, despite extensive research using schematic emotional faces in visual search tasks, it is still debated whether positive or negative schematic faces are processed more efficiently (e.g., Horstmann, Scharlau, & Ansorge, 2006). One main reason for the difficulties in interpreting results from this line of research is that visual search performance is not only determined by the target stimulus, but strongly modulated by interactions between properties of the target and the distractors (Duncan & Humphreys, 1989; Horstmann et al., 2006).

To rule out the influence of target-distractor similarities we measured detection performance for single negative and positive schematic emotional faces during CFS (Stein & Sterzer, 2012). Briefly, positive schematic faces overcame CFS more quickly than negative schematic faces. However, further experiments demonstrated that this effect was not related to stimulus valence, but due to the pronounced congruency between the mouth curve and the face contour in positive schematic faces. While these findings demonstrate the sensitivity of CFS to subtle differences in stimulus configurations and help to reconcile a number of discrepancies in the visual search literature, the most important implication is that schematic faces cannot be considered as well-controlled visual stimuli that differ only in terms of emotional meaning. Instead, the unnaturally exaggerated congruency between the mouth curve and the face contour in positive schematic faces which contrasts with the unnatural incongruency in negative schematic faces has introduced a new confound that affects detection performance.

As schematic faces additionally have limited ecological validity and because other recent studies revealed similar and additional stimulus confounds in schematic emotional faces (Becker, Anderson, Mortensen, Neufeld, & Neel, 2011; Coelho, Cloete, & Wallis, 2010; Horstmann, Becker, Bergmann, & Burghaus, 2010), future studies on the processing of emotional facial expressions could benefit from a return to naturalistic depictions of faces. It is possible that the influence of potential low-level confounds is not greater in well-controlled (e.g., contrast and luminance matched) photographs of emotional faces than in schematic depictions of emotional facial expressions.

2.3.3 The role of spatial frequency in rapid fear detection (Study 6)

In fact, these so-called "low-level" physical differences between facial expressions may actually represent the features that are key for discriminating between emotional facial expressions (Smith, Cottrell, Gosselin, & Schyns, 2005) and for eliciting perceptual biases such as rapid threat detection (Horstmann & Bauland, 2006). This would imply that a systematic manipulation of emotional faces along physical dimensions can reveal information used by the visual system to process such stimuli. Moreover, because different neurons are sensitive to distinct physical input, this approach can also be used to infer the neural pathways that process emotional faces.

The "standard hypothesis" (cf. Pessoa & Adolphs, 2010) of emotion processing in the human brain holds that the initial analysis of emotionally significant visual stimuli, and of stimuli signaling threat in particular, involves an extrageniculate subcortical pathway that projects from the retina to the amygdala via the superior colliculus and the pulvinar,

bypassing visual cortex (Tamietto & de Gelder, 2010). This subcortical "low road" (LeDoux, 1996) is assumed to enable the rapid processing of threatening stimuli such as fearful facial expressions. For example, the advantage of fearful compared to neutral faces in overcoming CFS has been attributed to the low road (Yang et al., 2007). However, although the idea of a subcortical pathway to the amygdala is now common textbook knowledge (Gazzaniga, Ivry, & Mangun, 2008), there is no anatomical evidence for a connection conveying visual information from the superior colliculus or the pulvinar to the amygdala in the primate brain (Pessoa & Adolphs, 2010).

Nevertheless, it is possible to test the functional role of the putative subcortical route psychophysically by manipulating the spatial frequency content of visual stimuli supposed to be processed along this pathway. Because visually responsive neurons in the superior colliculus receive afferents mainly from magnocellular ganglion cells conveying low spatial frequency (LSF) information, the low road is assumed to convey mainly coarse LSF information to the amygdala, whereas the processing of detailed high-spatial frequency (HSF) information involves cortical visual areas (Tamietto & de Gelder, 2010; Vuilleumier, Armony, Driver, & Dolan, 2003). To examine the functional role of this putative low road in the human visual system, we therefore measured detection performance for low- and high-pass filtered fearful and neutral faces (Stein, Seymour, Hebart, & Sterzer, in preparation).

Contrary to the purported role of an LSF-selective low road, across nine experiments we found the fear advantage to be specific to HSF information. First, the advantage of fearful relative to neutral faces in breakthrough from CFS was larger for HSF faces than for LSF faces. This HSF-specificity was independent of the spatial frequency of the masks and could not be explained by local contrast differences in the eye or mouth regions. Second, when we combined HSF and LSF information in hybrid faces, suppression durations were shorter for hybrids constructed from a HSF fearful face and an LSF neutral face than for hybrids containing an LSF fearful face and a HSF neutral face, even when the contrast of the HSF content was much lower than the contrast of the LSF content. Third, we replicated these findings from CFS using a sandwich masking paradigm.

These results suggest that there is no functional role of an LSF-sensitive subcortical pathway in mediating the fear advantage. Instead, the rapid detection of fearful faces relies on detailed HSF information processed by cortical circuits. This is consistent with research on expression recognition, showing that the discrimination of fearful facial expressions from other emotions relies virtually entirely on HSF information (Adolphs, Gosselin, Buchanan, Tranel, Schyns, & Damasio, 2005; Smith & Schyns, 2009). Moreover, recent findings from a patient with bilateral amygdala damage who nevertheless showed a significant fearful-face advantage suggest that the amygdala is not necessary for rapid fear detection (Tsuchiya et al., 2009). Together with our present findings in healthy observers, these results cast doubt on the existence of a subcortical pathway to the amygdala mediating rapid threat detection in the human visual system.

2.4 Detection during interocular suppression: A direct measure of unconscious processing? (Study 7)

All studies described so far used the duration of perceptual suppression induced by CFS to investigate the perceptual mechanisms that govern stimulus detection. However, when this method was first introduced, it was not supposed to index general detection performance, but to serve as a marker of unconscious processing under interocular suppression (Jiang et al., 2007). In this view, differences in suppression durations, for example for upright and inverted faces, reflect differential unconscious processing under interocular suppression, i.e. *CFS-*

specific unconscious processing differences. CFS-specific unconscious processing means that unconscious processing is present *because* CFS is applied to selectively interrupt conscious processing while leaving some unconscious processing intact. However, shorter suppression durations, for example for upright faces compared to inverted faces, could also be caused by generally lower thresholds for conscious detection independent of CFS-specific unconscious processing.

To rule out this possibility, a rapidly growing number of studies measuring detection during CFS have included a binocular control condition not involving interocular suppression. This control condition is supposed to mimic the perceptual experience under CFS and to measure potential threshold differences that are not specific to CFS (see Figure 1B; e.g., Costello et al., 2009; Jiang et al., 2007; Mudrik et al., 2011; Stein et al., 2011a, 2011b; Yang & Yeh, 2010; Zhou et al., 2010a). The absence of detection differences in this control condition is taken to imply that an effect obtained with CFS is caused by CFS-specific unconscious processing. Thus, whether differences in suppression durations are interpreted as reflecting differential unconscious processing under CFS depends on the outcome of the binocular control condition. Importantly, this conclusion rests on the premise that the comparison between the CFS and the control condition does indeed isolate CFS-specific unconscious processing and does not reflect any other factors that might differ between conditions. Whether this premise is valid, however, has not been previously tested. This question is important because recent studies showing that suppression durations can be modulated by semantic content in natural scenes (Mudrik et al., 2011) and even by concurrently presented odors (Zhou et al., 2010b) challenge current views on the scope and limits of processing without awareness (Lin & He, 2009).

In a series of six experiments, we made a first attempt to evaluate the validity of this novel approach to study unconscious processing during interocular suppression, using the effect of face inversion as an example (Stein, Hebart, & Sterzer, 2011a). Replicating previous reports, suppression durations were shorter for upright than for inverted faces. In addition, we obtained an FIE during CFS using non-speeded accuracy measures, thus ruling out that the upright face advantage was caused by differential response criteria for upright and inverted faces. Results also provided some evidence for an FIE in the binocular control condition, although in most experiments this effect was smaller than during CFS.

Most importantly, our study revealed marked differences between the CFS and the control condition that may render the comparison between the two conditions to infer CFS-specific unconscious processing invalid. First, we found large differences between the response time (RT) distributions from the two conditions, with much greater RT variability and a larger proportion of trials with very long RTs in the CFS condition. The distinct characteristics of the CFS and the control distributions may point to differences in the perceptual and cognitive engaged by face detection in the two conditions (Heathcote, Popiel, & Mewhort, 1991; Hockley, 1984; Ratcliff, 1979), perhaps resulting from the reduced predictability of stimulus appearance and greater temporal uncertainty in the CFS condition. Interestingly, in one experiment in which RT distributions were approximately matched, the size of the FIE did not differ between the two conditions. Second, trial-wise ratings of subjective face appearance showed that three different variants of binocular control conditions failed to resemble the perceptual experience under CFS.

These findings demonstrate that CFS and the binocular control condition differ on various dimensions other than CFS-specific unconscious processing, and thus call into question the notion that the comparison of these two conditions can provide unequivocal evidence for CFS-specific unconscious processing. Nevertheless, on a positive note, the

increased size of the effects obtained with CFS demonstrates that this method can be effectively used to measure potency of visual stimuli to gain access to awareness. In fact, such detection measures, independent of the specific experimental paradigm, are sometimes regarded as reflecting unconscious processing, because faster detection can only happen when the visual system discriminates stimuli before detection, i.e., unconsciously (Dijksterhuis & Aarts, 2003; Gaillard, Del Cul, Naccache, Vinckier, Cohen, & Dehaene, 2006).

2.5 Adaptation to facial features: The role of visual awareness (Studies 8 and 9)

To investigate unconscious processing specific to interocular suppression, however, other methods than visual detection during CFS are required. In the final two studies, we therefore adopted the well-established dissociation logic (Erdelyi, 1986) to examine whether invisible facial features – face shape and eye gaze directions – can be represented under CFS. In the dissociation paradigm, a direct measure of conscious awareness of a stimulus feature (e.g., detection, discrimination) is compared to an indirect measure of unconscious processing of the same feature (e.g., priming, attentional cueing effects). Unconscious processing is inferred when no perceptual sensitivity is found in the direct measure, but some sensitivity in the indirect measure.

Probing visual adaptation to stimuli suppressed from visual awareness provides one powerful means to trace the extent and limits of visual coding without awareness (Blake & He, 2005). Adaptation to basic visual features such as orientation, spatial frequency, motion, or color gives rise to visual aftereffects, referred to as the "psychologist's microelectrode" (Frisby & Stone, 2010), as such aftereffects are assumed to reflect the activity of neural populations responsive to the particular visual feature. Accumulating evidence demonstrates that adaptation to more complex stimuli, such as faces, can also result in highly specific aftereffects (Clifford & Rhodes, 2005). When presented under interocular suppression, basic visual features that are known to be processed in early visual cortical areas can induce aftereffects without visual awareness (Lin & He, 2009), whereas high-level aftereffects from visual adaptation to facial identity, age, and gender are eliminated when the adapting stimulus is rendered invisible by interocular suppression (Amihai, Deouell, & Bentin, 2011; Moradi, Koch, & Shimojo, 2005; Shin, Stolte, & Chong, 2009).

However, the absence of aftereffects from these specific facial attributes does not necessarily imply that all more complex visual representations related to facial information depend on visual awareness. Current multilevel accounts of interocular suppression (Sterzer et al., 2009; Tong et al., 2006) posit a gradual increase in the depth of suppression from early levels of the visual system that encode simple visual features to higher levels of visual processing that represent more complex and abstract stimulus properties (Nguyen, Freeman, & Alais, 2003; Sheinberg & Logothetis, 1997). Thus, it is possible that only high-level aftereffects that involve neural circuits located in anterior portions of the ventral visual pathway depend entirely on visual awareness, whereas more basic facial properties may be represented unconsciously. To test this hypothesis, in the first study we examined whether face shape aftereffects (Webster & MacLin, 1999) that rely on mid-level shape coding mechanisms (Jeffery, Rhodes, & Busey, 2006; Rhodes, Evangelista, & Jeffery, 2009) could be induced by adapting stimuli rendered invisible by CFS (Stein & Sterzer, 2011).

The second study (Stein, Peelen, & Sterzer, 2012a), in which we measured eye gaze adaptation during CFS, was motivated by the dual pathway model of face perception by Haxby and colleagues. In this model, changeable facial features (eye gaze, expression) are processed by the STS, while invariant facial features (identity) are processed by the lateral fusiform gyrus (Haxby et al., 2000). Interestingly, adaptation to suppressed emotional facial

expressions can result in significant aftereffects (Adams et al., 2010; but see Yang et al., 2010) and the STS responds more strongly to invisible fearful than to neutral faces, while no such effect is seen in fusiform gyrus activity (Jiang & He, 2006). Because both facial expression and eye gaze are processed by the STS (Calder et al., 2007; Haxby et al., 2000; Puce, Allison, Bentin, Gore, & McCarthy, 1998), we hypothesized that eye gaze directions could be capable of inducing aftereffects without awareness.

2.5.1 Face shape adaptation (Study 8)

Face shape adaptation aftereffects refer to the phenomenon that prolonged exposure to a distorted (contracted, expanded) adapting face makes a subsequently presented test face appear distorted in the opposite direction (Webster & MacLin, 1999) and is assumed to result from neural populations coding general face shape in a view-dependent fashion (Jeffery et al., 2006). The presentation of adapting faces under CFS yielded trials in which the adapting stimulus remained subjectively invisible and others in which the adapting face overcame suppression and became at least partially visible, presumably due to stochastic variations in the depth of interocular suppression (e.g., Blake & Logothetis, 2002). This allowed us to compare adaptation to invisible vs. partially visible face shape under constant physical stimulation. Control experiments ensured that participants could not discriminate the face shape of subjectively invisible adapting stimuli.

Across four experiments, we found that visual awareness of the adapting face resulted in larger face shape aftereffects (Stein & Sterzer, 2011). Invisible adapting faces induced aftereffects only when the adapting and the test face were presented to the same eye and in the same size. When the contribution of low-level, purely monocular mechanisms was ruled out by swapping the eye of stimulus presentation between the adapting and the test face, aftereffects were found only for subjectively visible adapting faces. Similarly, when the adapting and the test face were presented to the same eye but in different sizes, only partially visible adapting faces induced aftereffects. These results suggest that the representation of face shape requires awareness and that interocular competition as measured with CFS is resolved before the neural sites underlying mid-level visual representations of general face shape.

2.5.2 Eye gaze adaptation (Study 9)

In this final study, we adopted a similar design to test whether eye gaze aftereffects would be elicited by adaptation to invisible gaze directions (Stein et al., 2012a). Eye gaze aftereffects refer to observers' increased tendency to categorize a test face with averted gaze as looking straight ahead after adaptation to averted gaze in the same direction (Calder, Jenkins, Cassel, & Clifford, 2008; Jenkins, Beaver, & Calder, 2006). This effect is related to the adaptation of neural populations in the anterior STS that code left and right gaze directions, respectively (Calder et al., 2007).

In four experiments, we again found larger aftereffects when the adapting stimulus became at least partially visible. More importantly, when the adapting and the test stimulus were presented in identical sizes, we obtained aftereffects from subjectively invisible adapting stimuli. In contrast to face shape aftereffects from invisible adapting faces (Stein & Sterzer, 2011), these aftereffects from invisible eye gaze survived interocular transfer, suggesting that information about invisible gaze directions can be represented at levels of the visual system beyond purely monocular channels. However, introducing a size change between the adapting and the test stimulus eliminated aftereffects from invisible eye gaze. This indicates that size-dependent low-level properties of eye gaze directions can be processed unconsciously,

whereas size-invariant higher-level representations of eye gaze directions depend on visual awareness.

These results seem to be at odds with our previous study in which we found shorter suppression durations for faces with direct than with averted gaze (Stein et al., 2011c). One possibility is that this eye contact effect during CFS reflects a coarse signal associated with the arousal value of eye contact (Emery, 2000). Alternatively, the discrepancy between our two studies on eye gaze processing during CFS may be associated with the difference between a measure of visual detection of initially invisible stimuli and a measure of unconscious processing of stimuli rendered permanently invisible, as discussed in Section 2.4 (Stein et al., 2011a).

3 Conclusions and future directions

The nine studies that constitute this thesis suggest that (a) visual stimuli that are diagnostic for other individuals, i.e. upright human faces and bodies, have privileged access to awareness, (b) face detection follows newborns looking preferences but is also strongly modulated by visual experience with one's own social group, (c) eye contact results in faster face detection, (d) schematic emotional faces do not eliminate so-called low-level confounds, (e) rapid fear detection relies on high spatial frequencies, arguing against a functional role of a subcortical pathway to the amygdala, (f) visual detection during CFS cannot provide unequivocal evidence for unconscious processing specific to interocular suppression, and (g) only simple visual features can be represented when rendered permanently invisible by CFS, whereas high-level representations of face shape and eye gaze directions depend on visual awareness.

Because we discussed the findings of our studies alongside with the summary of the results in Section 2, this final part outlines only a few particularly important results within a broader context, points out limitations, and highlights how our findings may stimulate future research.

3.1 Face detection: Hard-wired or experience-derived?

Study 1 showed that face detection in adult observers relies on facial features similar to those governing newborns' looking preferences for faces (Stein et al., 2011b). Consistent with neonates' preference for upright over inverted faces (Farroni et al., 2005), upright faces rendered initially invisible by CFS were detected more quickly than inverted faces, replicating previous findings (Jiang et al., 2007). More importantly, this face inversion effect (FIE) was larger for faces that had normal contrast and were illuminated from above than for faces that were contrast reversed and illuminated from below. Moreover, schematic patterns consisting of three dark blobs were detected more quickly when the arrangement of these blobs respected the face-like configuration of the eyes and the mouth, and this effect was modulated by contrast polarity. These results are consistent with the notion of an inborn face template that is coarsely tuned to detect the configuration and contrast relationships of the eyes and the mouth in upright faces under natural lighting conditions (Johnson, 2005; McKone et al., 2007; Tomalski et al., 2009a).

This mechanisms, however, cannot account for the results from Study 2 in which the FIE was larger for faces from the observers' own race and age group than for faces from other race and age groups (Stein, End, & Sterzer, submitted). Whereas such own-race and own-age biases are well-known to influence face recognition (Meissner & Brigham, 2001; Rhodes & Anastasi, 2011), these findings provide the first evidence that social categories modulate the initial detection of a face. In principle, this modulatory influence of visual experience on face

detection can also be explained by template matching. However, this internal face representation would have to be finely tuned to the faces from one's own social categories. For example, to account for in-group advantages in face perception, Rossion and Michel (2011) proposed an experience-derived, holistic template face template representing an average of all known faces.

How can we reconcile the apparently discrepant results from Study 1, supporting the idea of a coarsely tuned inborn face template, and Study 2, suggesting that face detection involves a finely tuned experience-derived face template? Two specific data points from Study 1 may provide a hint. First, the FIE tended to be smaller for face-like patterns than for face photographs. Second, although newborns show no preference for upright vs. inverted face-like patterns with reversed contrast polarity (Farroni et al., 2005), we found a small, albeit statistically significant, inversion effect even for contrast-reversed face-like patterns. Thus, the more parsimonious explanation of our data is that visual awareness of faces relies on an experience-derived template. This detection mechanisms could be finely tuned to the structure and morphology of faces from one's own social groups – perhaps to an average face – but still provide a better fit to simple head-shaped patterns with an upright face-like blob configuration than to inverted blob configurations. Similarly, the reduced influence of inversion on the detection of faces under unnatural lighting conditions is consistent with an experience-shaped face detection mechanism.

This interpretation would imply that the perceptual mechanisms supporting visual awareness of faces are not hard-wired but adapted to our visual and social environment. Finally, it should be pointed out that although the idea of template matching in the case of structurally consistent visual patterns such as faces is appealing (Brunelli & Poggio, 1993; Lewis & Edmonds, 2003; Yuille, 1991), quite different mechanisms of face perception are conceivable (Dakin & Watt, 2009; Viola & Jones, 2004). Furthermore, a potential problem with template matching is that a single template may be not sufficiently flexible to detect faces from different viewing angles. As studies on human face detection have not yet investigated the detection of side views of faces (except for slightly angled faces, e.g. Figure 2), this is one possible avenue for future research.

3.2 Both upright faces and bodies have privileged access to awareness

In Study 3 we tested whether the mechanisms that govern access to awareness are specifically tuned only to upright faces (Zhou et al., 2010a), to all familiar object categories, or to visual information that is diagnostic for the presence of conspecifics, i.e. human faces and bodies (Stein et al., 2012b). Due to the strong impact of physical stimulus properties on suppression durations, it is virtually impossible to directly compare detection performance for stimuli from different object categories. We therefore again adopted the inversion paradigm, assuming that the comparison of suppression durations for identical stimuli in upright and inverted orientations can reveal detection mechanisms preferentially tuned to stimuli in their normal upright orientation. Our data showed large inversion effects for both human faces and bodies, suggesting that both upright human faces and upright human bodies have privileged access to awareness, whereas all other object categories, including chimpanzee faces and animals, yielded no or much smaller inversion effects (Figure 2).

It is interesting to relate these results to studies on face and body discrimination. Most experiments on discrimination (often used interchangeably with "recognition") use a sequential matching task in which participants indicate whether a stimulus exemplar is the same as or different from the previously presented stimulus exemplar. The disproportionate size of the FIE obtained in such tasks is one of the main sources of evidence for face

perception being "special" (McKone et al., 2007). Indeed, the FIE is more correlated in monozygotic than dizygotic twins, indicating that the inversion paradigm in face discrimination taps into heritable aspects of face processing (Zhu et al., 2010; also see Wilmer et al., 2010). Certainly, whether individual differences in conscious awareness of other persons also have a genetic basis – identical or different from the genetic basis of face recognition – is a fascinating question for future research.

In fact, Study 3 showed that the effect of inversion on detection differs in two important ways from the effect of inversion on discrimination. First, whereas the discrimination of individual faces is typically more strongly affected by inversion than the discrimination of body postures (Minnebusch & Daum, 2009), in our detection experiments the FIE and the body inversion effect (BIE) were of virtually equal size (see Figure 2). Second, while we found comparable effects of inversion for headless bodies and bodies with head contours only, the BIE in body posture discrimination tasks is critically dependent on head presence (Brandman & Yovel, 2010; Minnebusch, Suchan, & Daum, 2009; Yovel, Pelc, & Lubetzky, 2010). One possible reason for these differences is that faces are more important in discriminating other individuals than bodies, whereas faces and bodies may be similarly diagnostic for the presence of other persons (Bindemann, Scheepers, Ferguson, & Burton, 2010).

Finally, an important challenge for future research – also with regard to the distinct face detection mechanisms suggested by Studies 1 and 2 – will be to delineate the specific role of perceptual learning in the detection of conspecifics. Although the own-race and own-age biases observed in Study 2 demonstrate that visual experience fine-tunes detection mechanisms, a more specific account might posit that the privileged detection of upright faces and bodies results from expertise in discriminating individual faces and bodies (Gauthier & Tarr, 2002). Significant experience or training in individuating exemplars of an object category has been found to increase inversion effects in discrimination tasks (Diamond & Carey, 1986; Gauthier & Tarr, 1997), although even after decades of experience these effects continue to be smaller than the effect of inversion on the discrimination of faces (McKone et al., 2007; Robbins & McKone, 2007). Nevertheless, whether expertise in individuating objects can affect visual awareness of these stimuli is unknown and hence remains an exciting issue open to further investigation.

3.3 A subcortical pathway to the amygdala?

In designing some of our studies (Study 1, Stein et al., 2011b, and Study 4, Stein et al., 2011c), we adopted the "standard hypothesis" (cf. Pessoa & Adolphs, 2010) of a subcortical pathway from the the superior colliculus through the pulvinar to the amygdala (Johnson, 2005; Öhman, 2005; Tamietto & de Gelder, 2010) that processes emotionally and socially significant stimuli in a rapid, coarse, automatic and unconscious fashion. Indeed, the faster detection of faces with direct gaze than with averted gaze (Study 4) is consistent both with the purported function of this subcortical "low road" (LeDoux, 1996), i.e. to rapidly detect ecologically relevant visual information, as well as with current models of the processing of eye contact in the human brain (Senju & Johnson, 2009). Although it is interesting that a communicative signal such as eye contact influences visual awareness in the absence of low-level physical stimulus differences that are commonly associated with facial expressions, this effect of eye contact could also be mediated by enhanced processing along the geniculostriate pathway.

In Study 6 we directly addressed the functional role of a putative subcortical pathway to the amygdala (Stein, Seymour, Hebart, & Sterzer, in preparation). We tested the advantage of fearful over neutral faces in overcoming CFS, an effect that has been attributed to

processing along the low road (Yang et al., 2007). The subcortical pathway is assumed to receive mainly low spatial frequency (LSF) information, whereas high spatial frequency (HSF) image content is transmitted mainly by the geniculostriate pathway (Vuilleumier et al, 2003). However, in Study 6 we found the fear advantage to be specific to HSF information. These results are the exact opposite of what would be expected if the fear advantage was mediated by a LSF-sensitive subcortical pathway. Because Study 6 was designed to be consistent with the study by Yang et al. (2007), future studies are necessary to test whether similar results will be obtained with other measures such as attentional orienting (Tomalski et al., 2009b), with larger stimuli further in the periphery, or with other stimulus categories such as snakes (Öhman, Flykt, & Esteves, 2001).

Nevertheless, our findings are consistent with accumulating evidence that now challenges the dominant standard hypothesis of a "fear module" (Öhman & Mineka, 2001; Öhman, 2005) implemented in a direct subcortical pathway to the amygdala. As recently outlined by Pessoa and Adolphs (2010), there is neither direct anatomical nor other clear evidence for a connection conveying visual information from the pulvinar to the amygdala. Moreover, they point out that all findings widely cited as support for the standard hypothesis, such as rapid, unconscious fear processing, affective blindsight (de Gelder, Vroomen, Pourtois, & Weiskrantz, 1999) or amygdala activity without primary visual cortex (Morris et al., 2001; Pegna, Khateb, Lazeyras, & Seghier, 2004) are either consistent with enhanced processing along the geniculostriate and ventral visual pathways, or could involve anatomically established projections from the lateral geniculate nucleus or the pulvinar to visual cortical areas beyond primary visual cortex.

While these considerations call for a revised model of rapid threat processing, a puzzling finding is that one neuroimaging study found stronger amygdala activity to fearful than to neutral faces only for LSF faces but not for HSF faces (Vuilleumier et al., 2003). However, recent data from a patient with complete bilateral amygdala damage who showed a normal detection advantage for fearful faces (Tsuchiya et al., 2009) suggest that not only the notion of a low road to the amygdala but also the role of the amygdala role in the initial detection of fear needs to be revised.

3.4 How to interpret detection during interocular suppression?

In Study 7, we asked whether a measure of detection performance can reveal evidence for unconscious processing under CFS (Stein et al., 2011a). In some of our previous studies measuring suppression durations we included binocular control conditions, explicitly (Study 4) or rather implicitly (Studies 1, 3, and 5) following the prevailing view that a larger effect on detection performance in the CFS condition than in a binocular control condition not involving interocular suppression results from unconscious processing specific to CFS (e.g., Jiang et al., 2007; Mudrik et al., 2011). For this reasoning to be valid, the control condition needs to reflect all factors other than CFS-specific unconscious processing that influence detection performance in the CFS condition. In Study 7, we found marked differences between the two conditions that were not related to CFS-specific unconscious processing, but rather indicated that the control condition does neither match the perceptual experience during CFS nor the perceptual and cognitive processes engaged by detection during CFS. Furthermore, none of the published studies using this approach reported an effect in the control condition, suggesting that the gradual fade-in of a stimulus on top of the CFS masks (see Figure 1B) yields floor effects. We conclude that the comparison of detection during CFS to a binocular control condition cannot provide unequivocal evidence for CFS-specific

unconscious processing. Thus, the interpretation of effects obtained in previous studies needs to be reconsidered.

Nevertheless, the striking effects obtained with this method (see Section 1.2) call for an explanation, considering CFS-specific unconscious processing as only one possible mechanism. At present we and other researchers studying interocular suppression are faced with a "mystery" (R. Blake, personal communication, May 27, 2011) and can only speculate about the reason for the sensitivity of this method. We had hypothesized that the reduced predictability of stimulus appearance during CFS, perhaps being caused by stochastic processes similar to binocular rivalry (Blake & Logothetis, 2002), would lead to uncertainty and shifts in response criteria that could have affected suppression durations as measured by a speeded detection task. However, at least the difference in suppression durations between upright and inverted faces appears not to be caused by criterion effects, as we found a similar advantage for upright faces in accuracy-based unspeeded detection tasks with fixed presentation durations (Stein et al., 2011a).

Although this sensitivity to complex stimulus properties may point to the influence of CFS-specific unconscious processing, such high-level unconscious processing would be difficult to reconcile with studies adopting the dissociation paradigm. For example, suppression durations in Studies 1–7 were modulated by stimulus inversion, eye contact or category membership, whereas Studies 8 and 9 revealed the complete absence of visual adaptation to face shape (Study 8) and eye gaze directions (Study 9) rendered permanently invisible by CFS. Such discrepancies between methods, the uncertainties in reconciling results from different paradigms, and the ambiguous mapping of behavioral measures to unconscious and conscious processes underscores the need for clear, widely accepted and applied concepts, definitions, operationalizations and measures of unconscious and conscious processing.

4 List of research articles included in the thesis

This dissertation is based on the following research articles:

Study 1:

Stein, T., Peelen, M. V., & Sterzer, P. (2011). Adults' awareness of faces follows newborns' looking preferences. *PLoS ONE, 6*(12), e29361.

Study 2:

Stein, T., End, A., & Sterzer, P. (submitted). Social categories influence conscious vision: Own-race and own-age biases in face detection.

Study 3:

Stein, T., Sterzer, P., & Peelen, M. V. (2012b). Privileged detection of conspecifics: Evidence from inversion effects during continuous flash suppression. *Cognition*, Advance online publication. doi:10.1016/j.cognition.2012.06.005.

Study 4:

Stein, T., Senju, A., Peelen, M. V., & Sterzer, P. (2011). Eye contact facilitates awareness of faces during interocular suppression. *Cognition, 119*, 307-311.

Study 5:

Stein, T., & Sterzer, P. (2012, February 6). Not just another face in the crowd: Detecting emotional schematic faces during continuous flash suppression. *Emotion*, Advance online publication. doi: 10.1037/a0026944.

Study 6:

Stein, T., Seymour, K., Hebart, M. N., & Sterzer, P. (in preparation). Rapid fear detection relies on high spatial frequencies.

Study 7:

Stein, T., Hebart, M. N., & Sterzer, P. (2011). Breaking continuous flash suppression: A new measure of unconscious processing during interocular suppression? *Frontiers in Human Neuroscience, 5*, 167.

Study 8:

Stein, T., & Sterzer, P. (2011). High-level face shape adaptation depends on visual awareness: Evidence from continuous flash suppression. *Journal of Vision, 11*(8):5, 1-14.

Study 9:

Stein, T., Peelen, M. V., & Sterzer, P. (2012a). Eye gaze adaptation under interocular suppression. *Journal of Vision, 12*(7):1, 1-17.

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Eidestattliche Erklärung

Hiermit erkläre ich an Eides statt,

dass ich die vorliegende Arbeit selbständig und ohne unerlaubte Hilfe verfasst habe, dass ich mich nicht anderwärts um einen Doktorgrad beworben habe und keinen Doktorgrad in dem Promotionsfach Psychologie besitze, und dass ich die zugrunde liegende Promotionsordnung vom 3.8.2006 kenne.

Berlin, den 29.02.2012

Timo Stein